

WATER RELATIONS IN MILLIPEDES FROM SOME ALPINE HABITAT TYPES (CENTRAL ALPS, TYROL) (DIPLOPODA)

by

ERWIN MEYER

Institut für Zoologie, Universitätsstraße 4, A-6020 Innsbruck, Austria

&

GERHARD EISENBEIS

Institut für Zoologie, Saarstraße 21, D-6500 Mainz, F.R. Germany

ABSTRACT

Five species of millipedes, living either in a mixed oak wood (alt. 670 m) (*Enantiulus nanus*, *Mastigona mutabilis*) or in an *Alnus viridis* community (alt. 2000 m) (*Leptoiulus saltuagius*, *Haasea fonticulatorum* and *Ochogona caroli*) and the nival species *Trimerophorella nivicomis* are compared in respect of their desiccation tolerance and their capacity to take up water from moist substrate.

Results are expressed as the change of the initial water content of normally hydrated animals (Δm_0 , % h⁻¹) and as the rate of transpiration per unit surface area per unit time per saturation deficit ($\mu\text{g cm}^{-2} \text{h}^{-1} \text{mmHg}^{-1}$).

At 0% r.h. and at 25° C, *O. caroli* (44.6% h⁻¹), *M. mutabilis* (54.6) and *H. fonticulatorum* (65.5) lost their water at rates higher than *L. saltuagius* (9.1), *T. nivicomis* (9.8) and *E. nanus* (17.4). The tolerable water loss, expressed as a percentage of the initial body water, varied between 21% (*E. nanus*) and 44.2% (*L. saltuagius*).

The uptake of water by eversion of rectal tissue onto moist surface seems to be an important source of water gain. Dehydrated animals of *M. mutabilis* absorbed at a maximal rate of 79% h⁻¹. The ecological implications of these facts are discussed.

INTRODUCTION

Previous studies on water relations in millipedes indicate that resistance to desiccation is correlated with the distribution of the species and the microclimatic conditions in its habitat. This is well documented in a number of desiccation experiments with millipedes from tropical areas (Penteado & Mendes, 1982), desert zones (Crawford, 1972), grasslands (Baker, 1980), seashore and dune areas (Perttunen, 1953; Barlow, 1957), deciduous forests (O'Neill,

1969) and other humid habitats (Wegensteiner, 1982) or from a transect of different habitats in the Rhein-Main region (Haacker, 1968). One of the aims of the present study was to compare chordeumatid and julid species from three different habitats along a vertical transect in the Oetztal Alps in respect of their tolerance to desiccating conditions. It can be expected that the more extreme diurnal temperature variations and higher wind speed in the open highalpine grassland (Cernusca, 1976) may cause considerable stress, especially to species which live above the timberline.

As regards the ability of millipedes to take up water except by feeding or drinking the information is very scarce. Crawford (1972) reported that dehydrated specimens of *Orthoporus* can absorb water by extruding rectal tissue through the opened anal flaps onto moist soil. Investigations of the fine structure of the hindgut of the millipedes *Scaphiostreptus*, *Polydesmus* and *Glomeris* support the assumption that the rectal tissue plays an essential role in water balance of millipedes (Schlüter, 1979, 1980). The second aim of our study is to observe dehydrated animals having access to moist surfaces, to quantify their weight increase and to relate the absorption capacity to the species specific water loss rates.

MATERIALS AND METHODS

The six species (four Chordeumatida and two Julida) were collected at three sites along a vertical transect in the Oetz-

TABLE I

Biometrical data of the species investigated. Life mass- and total surface area figures represent the range among the investigated specimens. The surface area proportions and k -values are means (\pm S.E.)

| | n | Stadium | live mass w_0 (mg) | total surface area (mm ²) | surface area proportions (%) | | | k -value* |
|----------------------------------|---|---------|-------------------------|--|------------------------------|-----------------------|----------------------|-----------------------|
| | | | | | trunk | legs | antennae | |
| <i>Leptoiulus saltuvagus</i> | 6 | VIII-X | 11.4-34.8 | 52.0-138.6 | 69.4 (± 0.9) | 29.5 (± 0.9) | 1.1 (± 0.1) | 11.1 (± 0.5) |
| <i>Enantiulus nanus</i> | 5 | — | 7.3-29.9 | 30.9-120.7 | 77.5 (± 2.1) | 21.7 (± 2.1) | 0.8 (± 0.1) | 10.7 (± 0.8) |
| <i>Trimerophorella nivicomis</i> | 4 | IX | 6.9-11.8 | 46.3-64.2 | 57.5 (± 2.5) | 41.0 (± 2.4) | 1.5 (± 0.1) | 12.3 (± 0.3) |
| <i>Mastigona mutabilis</i> | 4 | VIII/IX | 13.5-22.4 | 59.1-102.6 | 52.2 (± 1.7) | 46.1 (± 1.6) | 1.7 (± 0.1) | 12.3 (± 0.6) |
| <i>Haasea fonticulatorum</i> | 5 | IX | 6.9-10.1 | 60.8-72.1 | 47.6 (± 2.3) | 50.9 (± 2.3) | 1.5 (± 0.1) | 15.9 (± 0.9) |
| <i>Ochogona caroli</i> | 5 | VII,IX | 1.4-5.7 | 15.3-48.3 | 50.5 (± 2.8) | 47.2 (± 2.9) | 2.3 (± 0.2) | 14.1 (± 0.8) |

* The species specific k -values were computed from the total surface area (S) and the live mass (w_0) using Meeh's formula: $S = k \cdot w_0^{0.667}$ (Loveridge, 1980).

tal Alps (Tyrol). *Enantiulus nanus* (Latzel) and *Mastigona mutabilis* (Latzel) from an inneralpine mixed oak wood (alt. 670 m) with a well-developed herb layer (Meyer et al., 1984); *Leptoiulus saltuvagus* (Verhoeff), *Haasea fonticulatorum* (Verhoeff) and *Ochogona caroli* (Rothenbühler) are dominant species in an *Alnus viridis* community (alt. 2000 m) near the timberline (Meyer, 1979; Meyer et al., 1984); *Trimerophorella nivicomis* (Verhoeff) is a nival species and was collected at a wind-swept ridge (Loiseleurieto-Cetrarietum, alt. 2500 m). Specimens were sampled by hand and kept in small boxes containing a one cm layer of tap water agar, soil and dead plant material from their habitat. To prevent condensation it was important to perforate the covers of the boxes. The rearing temperatures varied between 10-15° C.

The transpiration experiments were made at the Institute of Zoology (University of Mainz) with an apparatus for continuous recording of the weight changes (Eisenbeis, 1982). For measuring the weight losses the animals were enclosed in a small wire-netting cage and exposed to different relative humidities in a glass vial. The small cages were suspended directly by thin wires from the underfloor balance (Sartorius electrobalance 4431, sensitivity 1 µg). Relative humidities were adjusted with saturated salt solutions (Winston & Bates, 1960). The glass vials were placed in a flow-through water bath to keep the temperature constant. Prior to testing the millipedes had not to be starved, as the weight loss via defecation did not influence the recorded linearity of the transpiration rates. As no

manipulation (e.g. sealing of spiracular openings, mouths, anus) on the animals were made, weight losses resulting from this procedure may obviously be attributed to a combination of cuticular and respiratory water loss. Even repugnatorial gland secretion could be observed by the coloration of P₂O₅.

Immediately after the transpiration experiments the dehydrated animals were maintained on wet filter paper in petri dishes for the absorption experiment. Their weight gain was measured to one µg with a mechanical microbalance (Sartorius 2405) at irregular intervals.

The effective surface area of the six species was estimated by drawing the outlines of the trunk (incl. head), one leg and one antenna in lateral view using a Wild stereo microscope with a drawing mirror and measuring the area by planimetry. From the total surface area of the specimen the value of k in the formula $S = k \cdot w_0^{0.667}$ (Loveridge, 1980) was computed. Since k is a species-specific constant the surface area (S) of any other member of the same species could be calculated from its weight (w_0). Transpiration rates are expressed either as percentage loss of original water mass (m_0) or as water loss per unit surface area per saturation deficit. The water content (m_0) of the animal was calculated as the difference between the original weight of the fully hydrated animal (w_0) previous to the experiment and its dry weight (70° C, P₂O₅) after being killed following the transpiration and absorption experiments.

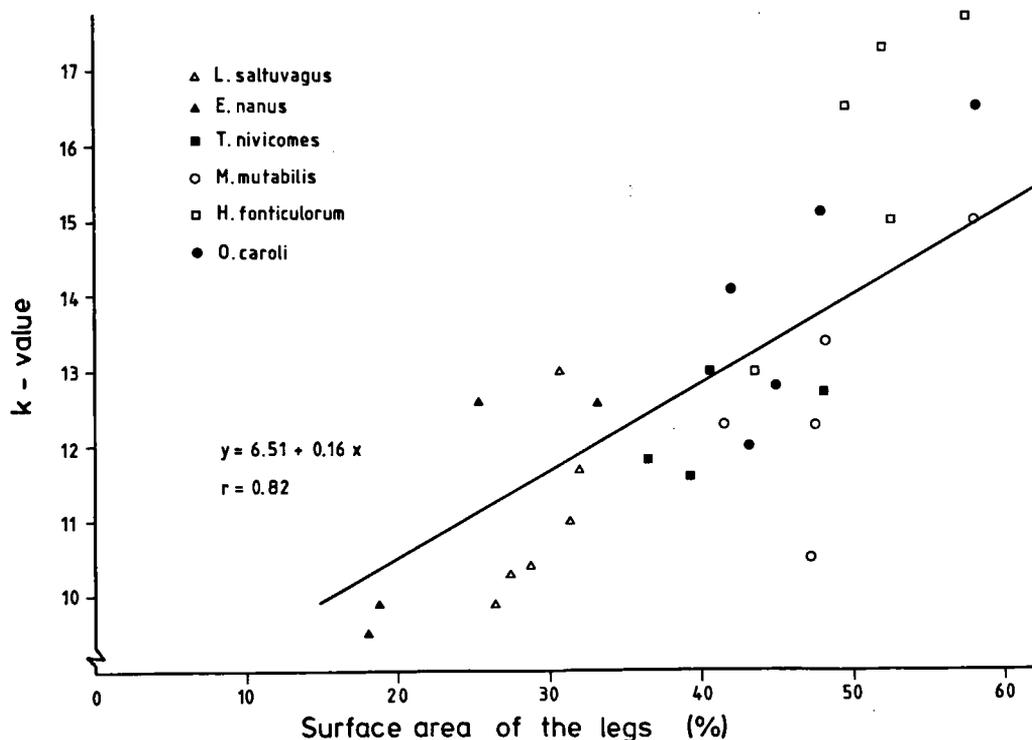


Fig. 1. *K*-values as a function of surface area proportions of the legs in six species of millipedes.

RESULTS

Biometrical data of the species

Masses, surface areas and calculated *k*-values for the six species are given in table I. The *k*-values cover a wide range. The smallest value (10.7) could be observed for the julid *E. nanus*, the highest (15.9) for the chordeumatid *H. fonticulatorum*.

A possible explanation for the great variety of the *k*-values arises from the surface area proportions of the body parts. If the leg surface proportions are brought in relation to the corresponding *k*-value of a given specimen (fig. 1) the points fit to a straight line with a regression coefficient of 0.82. But the *k*-values diverge considerably from the line if the leg surface proportions reach the upper limit (> 50%).

Nevertheless the *k*-values seem to be highly dependent from the proportions of the legs with respect to the total surface area of a specimen.

Without the legs the range of the species-specific *k*-value would be much smaller, between 6.3 (*M. mutabilis*) and 8.8 (*E. nanus*). As pointed out by Loveridge (1980) one should therefore ask to which extent water loss does occur through such appendages when calculating surface-specific transpiration rates from weight-specific data. The only *k*-value known for other millipedes was recorded by Cloudsley-Thompson (1950) who investigated the surface area of the paradoxosomatid *Paradesmus gracilis* (C. L. Koch) (= *Oxidus g.*) ($k = 15$) in a comparable way.

Water content and tolerance of water loss

As can be seen from published data (e.g. Barlow, 1957; Edney, 1977; Baker, 1980; Meyer, 1980) the water content of millipedes is very variable, both within and between species. Several causes of variations in the water content are given, e.g. stage, sex, differences in fat deposition or gut content and season.

TABLE II

Water content as percent of live mass (w_0) and tolerable water loss as percent of original water (m_0) in the millipedes investigated.

| | n | Water content (%) | | highest tolerable water loss | |
|----------------------------------|----|-------------------|-------------|------------------------------|---------------|
| | | \bar{x} | range | as % of m_0 | as % of w_0 |
| <i>Leptoiulus saltuagus</i> | 16 | 61.2 | (55.2-79.2) | 44.2 | 35.2 |
| <i>Enantiulus nanus</i> | 6 | 66.6 | (60.8-74.0) | 21.1 | 14.0 |
| <i>Trimerophorella nivicomis</i> | 1 | 61.6 | — | 32.2 | 19.8 |
| <i>Mastigona mutabilis</i> | 2 | 70.5 | (70.2-70.7) | 35.7 | 25.2 |
| <i>Haasea fonticolorum</i> | 4 | 69.7 | (64.9-74.0) | 35.6 | 26.2 |
| <i>Ochogona caroli</i> | 9 | 67.3 | (64.0-76.1) | 42.5 | 28.6 |

The biological significance of the water content may become more evident when it is seen in relation to the tolerable water loss (table II). As defined for the present study the extent of dehydration was tolerable if that animal was able to rehydrate to its original weight on moist filter paper. Table II shows the water content (mean and extremes) and the maximal tolerable water loss which could be observed for a species. The differences of the water content are greater within species than between species. In *L. saltuagus* the specimen with the highest water content was an XIth female, in *O. caroli* a newly moulted adult female.

From the present observations it is not apparent whether animals with the highest water content are also most tolerant to water loss. Nevertheless it seems remarkable that all species (*E. nanus* excepted) tolerate a loss of more than one third of their original water. It should be stressed that this amount of water loss was tolerable in a biological sense. Perttunen (1953), Barlow (1957), Haacker (1968), Stewart & Woodring (1973) and Penteadó & Mendes (1982) reported tolerable weight losses up to a maximum of 75% (*Julus scandinavicus* Latzel). But in those cases the animals were near death and completely immobile.

The effect of ambient humidity on water loss

As pointed out above, the transpiration experiments were made with a continuous record-

ing electrobalance. In each case the animals were exposed to a series of five humidities (99, 95, 76, 34 and 0 % r.h.), beginning with the highest at a constant temperature. The following components could be distinguished on the recorder paper:

- a high initial weight loss immediately after the exposure of the animal,
- a long linear period with a constant rate of water loss,
- an exponential decrease of transpiration, when animals had obviously lost all the original water.

The same sequence of weight loss has been demonstrated by Eisenbeis (1983) for a number of soil arthropods. According to the hygroscopic properties of the cuticle (Loveridge, 1980) the initial water loss may be due to loss of hygroscopic water. This period lasted at most five to ten minutes. Subsequently the rate of water loss was constant and related to the saturation deficit. The final exponential component was only recorded in long term experiments when animals had lost about 50% of the original water. In *O. caroli* once the transpiration was still linear even after a water loss of 54%.

Fig. 2 shows the results of the transpiration experiments, expressed as proportions of the original water content. These percent transpiration rates indicate remarkable differences between the species. At 0% r.h. and at 15° C the

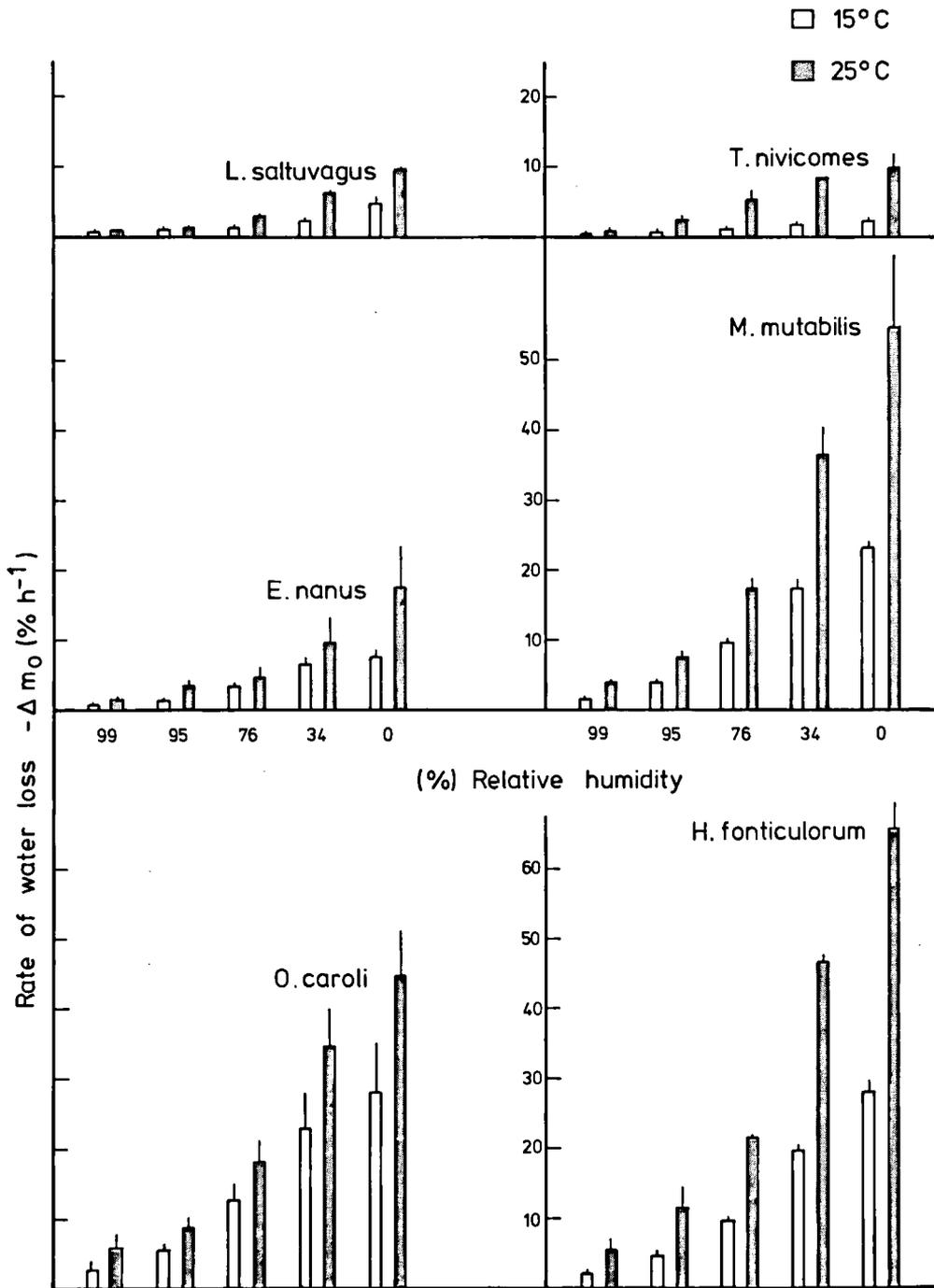


Fig. 2. Comparative water loss rates as percent of original water (m_0) at certain relative humidities at 15° and 25° C in six species of millipedes. Vertical lines represent S.E., n see table V.

water content of *T. nivicomis* is reduced with a rate of 2.1 % h⁻¹. In contrast the water loss rates of the other three chordeumatid species (*M. mutabilis*, *H. fonticulatorum*, *O. caroli*) were considerably higher (22.7-27.9%).

In all the species water loss increased more than ten times when the ambient humidity was lowered from 99% to 0% r.h. Table II gives the possible limits of the tolerance to depletion. When these figures are related to the water loss, given in fig. 2, one may calculate how long a species can maintain its vitality at a given ambient humidity without having access to any source of water. The result is shown in table III.

TABLE III

Period of time (in hours) after which animals have lost the critical amount of water in different relative humidities and at 15° C. The figures are calculated by combination of the species-specific water loss (Δm_p , %/h) (fig. 2) and the tolerable water loss (table II).

| % r.h. | 99 | 95 | 76 | 34 | 0 |
|----------------------------------|-----|----|----|----|----|
| <i>Leptoiulus saltuvagus</i> | 111 | 88 | 37 | 19 | 9 |
| <i>Enantiulus nanus</i> | 42 | 18 | 7 | 3 | 3 |
| <i>Trimerophorella nivicomis</i> | 161 | 81 | 40 | 20 | 15 |
| <i>Mastigona mutabilis</i> | 22 | 9 | 4 | 2 | 2 |
| <i>Haasea fonticulatorum</i> | 17 | 9 | 4 | 2 | 1 |
| <i>Ochogona caroli</i> | 16 | 8 | 3 | 2 | 2 |

The data at 0% r.h. are of theoretical value only, since such conditions do not occur in the field. But in the wind-swept *Loiseleuria* heath, the natural habitat of *T. nivicomis*, relative humidities were measured as low as 50% (Cernusca, 1976). Under these conditions *T. nivicomis* should survive at least 20-40 hours without water gain, but the litter-dwelling chordeumatid species only 2-4 hours. *L. saltuvagus* shows in the dwarf shrub communities at certain periods a high locomotory activity (Meyer, in press) corresponding well with its relatively high tolerance time of 19-37 hours. The litter dwellers *M. mutabilis*, *H. fonticulatorum*, and *O. caroli* would maintain their vitality only 16-22 hours, even at 99% r.h.

To eliminate the effect of different size of the animals and the effect of saturation deficit on the rate of transpiration at a given temperature, water loss data, shown in table IV and fig. 3, were calculated as μg water loss per unit surface area per unit time per saturation deficit. Although we know that other (e.g. respiratory) than cuticular water losses are included, these figures may be used to compare the permeability of the integument.

Again, the highalpine species *T. nivicomis* shows lowest permeability (18.3, at 15° C and at 0% r.h.). The water loss of *H. fonticulatorum* and *O. caroli* from alder litter is about tenfold (170-183). In *M. mutabilis* living in oak litter the permeability of the integument seems to be highest (235).

As indicated in fig. 3 permeabilities are not constant, they vary with saturation deficit. In four of the six species the permeability of the integument seems to decrease about sevenfold as ambient humidity falls from 99% to 0%. Even higher is the change of the permeability in *O. caroli* and *T. nivicomis*. As discussed by Edney (1977) the change in permeability may be due to the decreasing hydration of the cuticle and is certainly widespread and general among terrestrial arthropods (Eisenbeis, 1983 and unpubl.).

The effect of temperature on water loss

As only two experimental temperatures (15° and 25° C) were employed the effect of temperature on transpiration rates could not be observed satisfactorily. According to fig. 2 a raise in temperature from 15° to 25° C may result in transpiration rates doubled or tripled. The highalpine *T. nivicomis* seems to be more sensitive to higher temperatures. Its water loss rises about six times (from 15° to 25° C).

As regards the permeability of the integument and its relationship to temperature the results are more complex (fig. 3), as they depend on the ambient humidity. At 99% r.h., in some cases also at 95% r.h., the integument seems to be more permeable at 15° C than at 25° C. At lower humidities transpiration rates are probably equal at both temperatures or

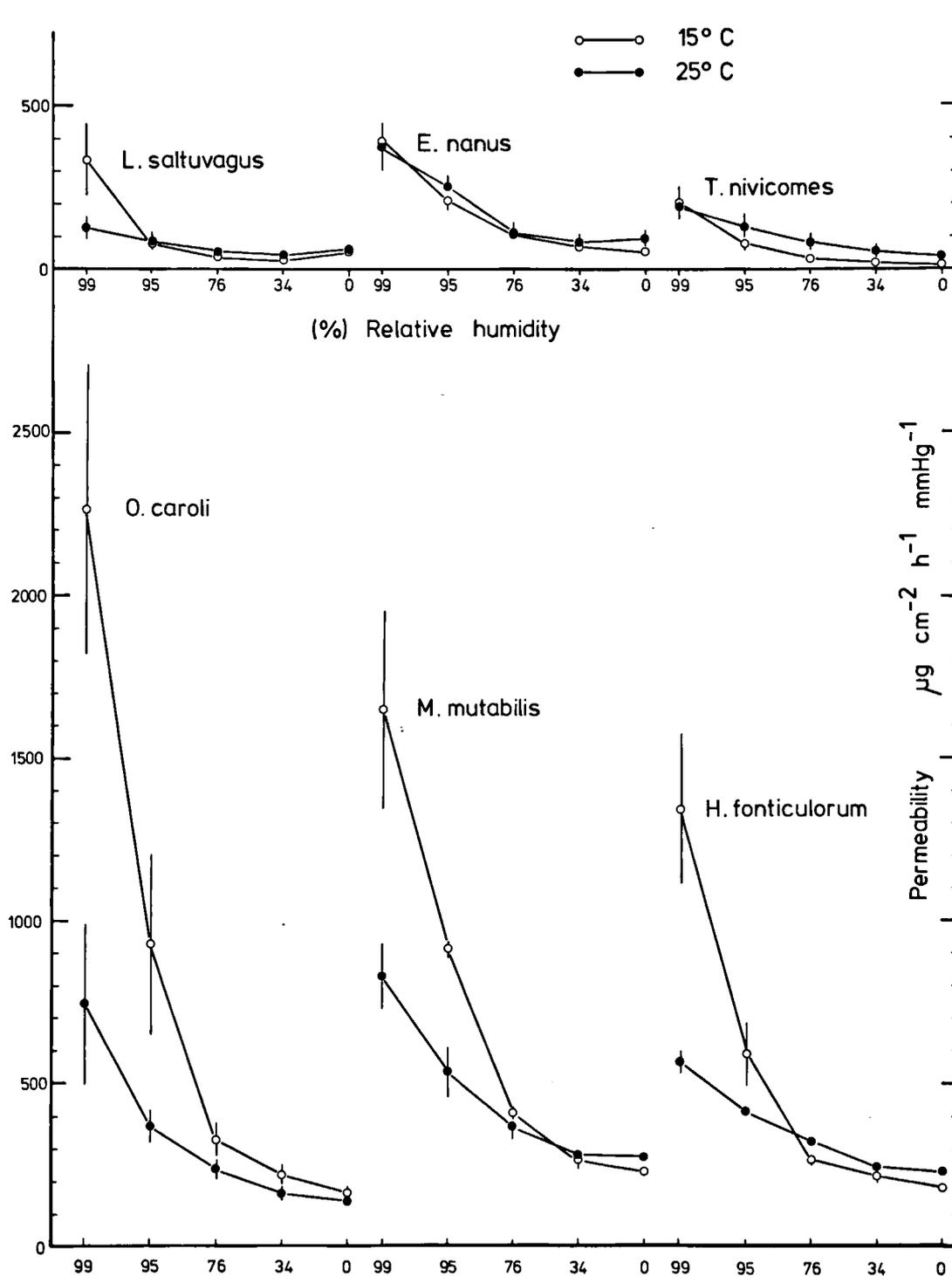


Fig. 3. Change of the permeability in relation to ambient relative humidity in six species of millipedes at 15° and 25° C. Vertical lines represent S.E., *n* see table IV. The difference between the permeabilities at 15° and 25° C is significant ($p \leq 0.05$, Mann-Whitney U-test) in *O. caroli* at 99% and 95% r.h., *M. mutabilis* at 99% and 95% r.h., *H. fonticulatorum* at 99% and 95% r.h., *L. saltuvagus* at 99% r.h., *T. nivicomes* at 76%, 34% and 0% r.h.

TABLE IV

Rates of water loss investigated in millipedes from various habitats at 0% r.h. and at 15° and 25° C.

| | habitat (alt.) | n | 15° C | | 25° C | |
|----------------------------------|-----------------------------------|---|---|--------------------|--|--------------------|
| | | | permeability (± S.E.) | resistance* | permeability (± S.E.) | resistance |
| | | | $\mu\text{g cm}^{-2} \text{h}^{-1}$ mmHg^{-1} | s cm^{-1} | $\mu\text{g cm}^{-2} \text{h}^{-1}$ mm Hg^{-1} | s cm^{-1} |
| <i>Enantiulus nanus</i> | oak litter (670 m) | 3 | 53.4 (± 4.0) | 63.7 | 98.1 (± 25.1) | 34.7 |
| <i>Mastigona mutabilis</i> | oak litter (670 m) | 3 | 234.8 (± 10.0) | 14.5 | 284.8 (± 55.9) | 11.9 |
| <i>Leptoiulus saltuvagus</i> | alder litter (2000 m) | 7 | 53.7 (± 13.8) | 63.3 | 55.5 (± 6.8) | 61.3 |
| <i>Haasea fonticulorum</i> | alder litter (2000 m) | 3 | 185.0 (± 11.7) | 18.4 | 236.9 (± 13.9) | 14.4 |
| <i>Ochogona caroli</i> | alder litter (2000 m) | 6 | 169.8 (± 17.7) | 20.0 | 147.0 (± 17.2) | 23.1 |
| <i>Trimerophorella nivicomis</i> | high alpine grassland (2500 m) | 3 | 18.3 (± 1.8) | 185.9 | 45.9 (± 9.5) | 74.1 |

* Resistance (s cm^{-1}) is the reciprocal of permeability (cm s^{-1}). A quick rule of thumb for the conversion of $\mu\text{g cm}^{-2} \text{h}^{-1} \text{mmHg}^{-1}$ to cm s^{-1} is given by the relationship: $2.94 \cdot (\mu\text{g cm}^{-2} \text{h}^{-1} \text{mmHg}^{-1}) = (\text{cm s}^{-1}) \cdot 10^4$ (Edney, 1977: 231).

slightly higher at 25° C. As investigated by Cloudsley-Thompson (1950) and Crawford (1972) in *Paradesmus gracilis* and *Orthoporus ornatus* (Girard), cuticular permeabilities change remarkably only above 30° C.

Uptake of water

The possibility of water uptake via the anus was suggested and demonstrated by Crawford (1972) for *Orthoporus ornatus* by adding an aqueous solution of crystal violet to the soil adjacent to the extruded rectum of a millipede. In the present study the dehydrated animals were allowed to recover on moist filter paper. The extrusion of rectal tissue was observed with a stereo microscope. The amount of extrusion in an VIIIth stadium female of *M. mutabilis* is shown in two scanning electron micrographs (fig. 4).

Soon after having contact with the wet filter paper all species everted the rectal tissue onto the moist surface. The duration of the contact

varied and was interrupted by moving around and searching new dark places. Therefore the amount of water gain per hour does not relate to the exact contact time of the rectal tissue to the moist surface.

Table V indicates the highest observed weight increases which could be observed between two weight controls. The results are expressed as percentage gain of the original water and are comparable with the corresponding water loss rates. *M. mutabilis*, which is able to absorb 79.4% of its original water in one hour has the highest rate of water uptake. High absorption rates were measured also for *T. nivicomis*, *O. caroli* and for *L. saltuvagus* (64.2-50.1 % h⁻¹). Only *E. nanus* (19.0) and *H. fonticulorum* (19.2) seem to be less effective in rehydration when desiccated. From table V it appears that there is no reason to suggest a close relationship between transpiration and absorption rates. *T. nivicomis*, with highest resistance against water loss shows a considerably high absorption capacity.

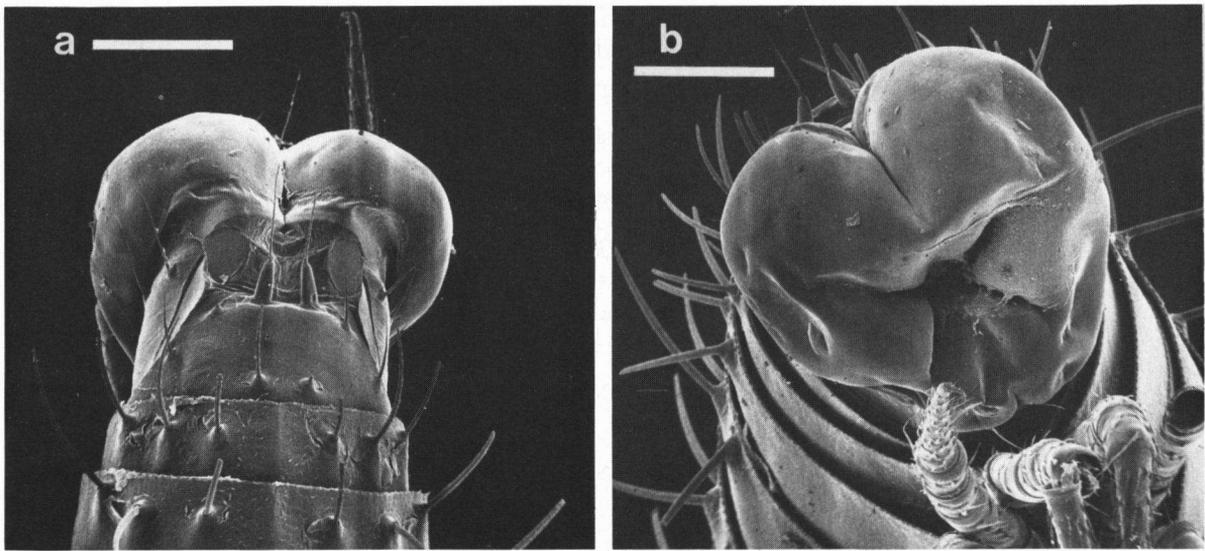


Fig. 4. Scanning electron micrographs of everted rectal tissue in an VIIIth stadium female of *Mastigona mutabilis*: a, dorsal; b, ventrocaudal view. Scale 0.2 mm.

DISCUSSION AND ECOLOGICAL IMPLICATIONS

Transpiration rates of millipedes of different orders and from various habitats are compared in table VI. The results are expressed either as percent loss of original water or absolute water

loss per unit surface area per unit time per saturation deficit. *M. mutabilis* from the humid oak litter has a transpiration rate a hundred times greater than the desert millipede *Orthoporus*. In general, chordeumatid species seem to be less tolerant to desiccating conditions than species of other orders. Not included in table VI

TABLE V

Water loss rates (at 0% r.h. and at 25° C) and highest observed rates of water uptake from moist filter paper (at 25° C). Both loss and uptake rates are expressed as percent of original water (m_0).

| | water loss (\pm S.E.) | | water uptake | |
|----------------------------------|------------------------------------|----------|------------------------------------|----------|
| | $-\Delta m_0$ (% h ⁻¹) | <i>n</i> | $+\Delta m_0$ (% h ⁻¹) | <i>n</i> |
| <i>Leptoiulus saltuagus</i> | 9.1 (± 0.3) | 4 | 50.1 | 5 |
| <i>Enantiulus nanus</i> | 17.4 (± 5.8) | 3 | 19.0 | 5 |
| <i>Trimerophorella nivicomis</i> | 9.8 (± 2.1) | 3 | 64.2 | 4 |
| <i>Mastigona mutabilis</i> | 54.6 (± 10.2) | 3 | 79.4 | 5 |
| <i>Haasea fonticulatorum</i> | 65.5 (± 3.6) | 2 | 19.2 | 4 |
| <i>Ochogona caroli</i> | 44.6 (± 6.5) | 4 | 57.6 | 5 |

TABLE VI

Recorded rates of water loss in millipedes from different orders in dry air (0% r.h.). Glomerida: 4; Polyzoziida: 8; Spirostreptida: 3, 15; Julida: 6, 9 (= *Leptophyllum n.*), 11, 13, 14 (= *Schizophyllum s.*); Chordeumatida: 1 (= *Heteroporatia m.*), 2 (= *Orobainosoma f.*), 5 (= *Triakontazona c.*), 12; Polydesmida: 7 (= *Oxydesmus p.*), 10 (= *Paradesmus g.*).

| | temp. ° C | water loss (± S.E.) | | ref. |
|--|--------------|---------------------------------------|--|------------------------------|
| | | -Δm _o (% h ⁻¹) | μg cm ⁻² h ⁻¹ mmHg ⁻¹ | |
| 1 <i>Mastigona mutabilis</i> (Latzel) | 25 | 54.6 (± 10.2) | 284.8 (± 55.9) | present study |
| 2 <i>Haasea fonticulatorum</i> (Verhoeff) | 25 | 65.5 (± 3.6) | 236.9 (± 13.9) | present study |
| 3 <i>Ophistreptus</i> sp. | 30 | — | 226.2 * | Cloudsley-Thompson (1959) |
| 4 <i>Glomeris marginata</i> (Villers) | 26 | — | 200 | Edney (1977) |
| 5 <i>Ochogona caroli</i> (Rothenbühler) | 25 | 44.6 (± 6.5) | 147.0 (± 17.2) | present study |
| 6 <i>Tachypodoiulus niger</i> (Leach) | 30 | — | 135.1 * | Cloudsley-Thompson (1959) |
| 7 <i>Coromus platycercus</i> (Attems) | 30 | — | 119.4 * | Cloudsley-Thompson (1959) |
| 8 <i>Polyzoniium germanicum</i> Brandt | 30 | 18.0 | — | Wegensteiner (1982) |
| 9 <i>Enantiulus nanus</i> (Latzel) | 25 | 17.4 (± 5.8) | 98.1 (± 25.1) | present study |
| 10 <i>Oxidus gracilis</i> (C. L. Koch) | 26 | 5.3-7.1 | — | Perttunen (1953) |
| | 30 | — | 94.3 * | Cloudsley-Thompson (1959) |
| 11 <i>Leptoiulus saltuivagus</i> (Verhoeff) | 25 | 9.1 (± 0.3) | 55.5 (± 6.8) | present study |
| 12 <i>Trimerophorella nivicomis</i> (Verhoeff) | 25 | 9.8 (± 2.1) | 45.9 (± 9.5) | present study |
| 13 <i>Julus terrestris</i> Linnaeus | 26 | 8.3 | — | Perttunen (1953) |
| 14 <i>Ommatoiulus sabulosus</i> (Linnaeus) | 26 | 0.9-7.2 | — | Perttunen (1953) |
| 15 <i>Orthoporus ornatus</i> (Girard) | 30 | 0.1-0.3 | 2.8-7.9 | Crawford (1972) |

* From Crawford (1972).

are values from Haacker (1968) and O'Neill (1969). Their results indicate a higher sensitivity to moisture stress for chordeumatid species as well.

Surprisingly transpiration rates of the highalpine *T. nivicomis* are next to the eurytopic species *Julus terrestris* Linnaeus and *Ommatoiulus sabulosus* (Linnaeus). This may lead to the assumption that highalpine species should have a greater tolerance to desiccating conditions. Differences in tolerance to water loss may also facilitate ecological isolation within the same

habitat. *O. caroli* and *H. fonticulatorum* coexist in alder litter. Their activity patterns, life cycles and densities are nearly the same (Meyer, 1979). The present results show that according to their differences in tolerance to desiccation stress they are probably slightly isolated by microhabitat.

Recovery of dehydrated animals on wet filter paper could be demonstrated among all species investigated. Also it could be observed that rectal tissue was everted and touched down onto

wet surface. Ultrastructural studies by Schlüter (1979, 1980), Rosenberg (1983, 1984) and Rosenberg & Bajorat (1983) reveal that the rectum of millipedes and the anal and coxal organs of centipedes function in fluid absorption. The cuticle of these organs is covered with a distinct mucous layer secreted by exocrine glands. This mucus is expected to be hygroscopic and functioning as a carrying fluid. Water vapour absorbers among insects have comparable condensing fluids directly involved in absorbing the condensate (Machin et al., 1982).

It can be concluded that water uptake via the rectum is an essential source of water gain in millipedes, enabling the animals to compensate for continuous cuticular and respiratory water loss. This fact seems to be important as at high ambient humidity the cuticle is more permeable. It should be stressed that *M. mutabilis*, the species with the highest absorption capacity, has the highest permeability of the integument. It may be expected that a morphometric analysis will relate absorption capacity to active surface of rectal tissue. The different sizes of the everted "rectal bladders" observed support this assumption.

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